THE DINOCEPHALIAN MANUS AND PES

By

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(With 10 Text-figures)

Contents

Introduction

Very little is known of the feet of the South African Dinocephalia.

From a mixed lot of disarticulated elements Gregory produced the mount of *Moschops*, which includes the reconstructed feet, but in his description of 1926 admits his inability to assemble either foot.

In 1929 Broom described the two proximal tarsal elements of *Jonkeria*.

In 1940 Byrne very briefly described both the fore- and hindfeet of *Moschoides*.

In 1954 I described a partial Moschopid carpus and gave descriptions and figures of the fore- and hindfoot of *Micranteosaurus*, which I at the time completely misinterpreted.

From the Russian deposits Orlov in 1958 described and gave beautiful figures of both fore- and hindfeet of *Titanophoneus*.

Material

After 35 years of collecting in the *Tapinocephalus* zone, during which period I have excavated two hundred and fifty-one specimens of the Dinocephalia, I

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have a poor collection of foot material. This is due to the nature of the preservation of the Dinocephalian material in this zone. I know of only one case where a skeleton more or less articulated has been found. In all other cases the bones of the skeleton are disarticulated and scattered with the loss of most of the smaller elements composing the feet.

SAM 4323 *Micranteosaurus parvus*. An incomplete fore- and hindfoot associated with a good snout.
Merweville Commonage, Low *Tapinocephalus* zone. Coll. Haughton 1917.

SAM 9157 *Moschops*? An incomplete carpus associated with a humerus, ulna and radius.
Wolwefontein, Prince Albert, Low *Tapinocephalus* zone. Coll. Boonstra 1929.

SAM 12011 *Struthiocephalus*? Tibia and astragalus.
Rietfontein, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.

SAM 12017 Tapinocephalian. A calcaneum and fibula with a piece of skull.
Spitskop, Laingsburg. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.

SAM 12033 Tapinocephalian. Radiale.
Worsteling, Laingsburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1956.

SAM 12065 *Struthiocephalus*? Two calcanei found on a small slope which yielded a lot of bones together with some cranial material of *Struthiocephalus*.
Skoenmaker, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra 1957.

SAM 12104 Titanosuchian. An isolated astragalus.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.

SAM 12105 Titanosuchian. An isolated astragalus.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.

SAM 12109 Titanosuchian. An isolated radiale.
Kalkkraal, Prince Albert. Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.

SAM 12110 Titanosuchian? Radius and intermedium.
Kalkkraal, Prince Albert, Low *Tapinocephalus* zone. Coll. Boonstra and Zinn 1957.

SAM 12210 Titanosuchian. An isolated astragalus.
Kroonplaas, Beaufort West. High? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959.

SAM 12226 *Struthiocephalus* sp. Hindfoot and manus associated with some teeth.
Knoffelfontein, Beaufort West. Coll. Boonstra and Zinn 1959.

SAM K201 *Struthiocephalus* sp. Isolated astragalus.
Paradys of Rietfontein, Prince Albert. Middle *Tapinocephalus* zone. Coll. Boonstra 1959.

SAM K249 *Parascapanodon* sp. Disarticulated skeleton without skull, including two calcanei, one astragalus and other carpal, tarsal and digital bones.
Steynskraal, Beaufort West. Middle *Tapinocephalus* zone. Coll. Boonstra and Zinn 1959.

SAM K271 Tapinocephalian. Isolated calcaneum and astragalus.
Wonderboom of Plaatdorings, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Boonstra, 1960.

SAM K323 Tapinocephalian. Scattered foot bones associated with teeth.
Die Bad, Beaufort West. Low *Tapinocephalus* zone. Coll. Boonstra, Zinn and Gow, 1960.

SAM K362 Tapinocephalian. Disarticulated carpals, tarsals and phalanges associated with cranial and dental material.
Twee Susters of Grootfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962.

SAM K366 Moschopid? Isolated Calcaneum.
Moutonsfontein, Fraserburg. Low? *Tapinocephalus* zone. Coll. Boonstra and Zinn 1962.

Forefoot

Tapinocephalia (Fig. 1)

With so little and such poor material available only a tentative description can be given of the Tapinocephalian manus. Of the seven specimens in which elements of the forefoot are preserved four have only disarticulated carpal and digital bones preserved. In SAM 9157 parts of four proximal carpals are present in articulation; in Romer's Chicago specimen of *Moschoides* (which I have not seen) an articulated manus is preserved and in SAM 12226 an incomplete and partially disarticulated manus of a species of *Struthiocephalus* is available for study.

The Tapinocephalian manus is broad and very short with little difference in the length of the toes, but the fourth is the longest digit. The purchase of the foot is thus mainly mesaxonic but somewhat more post- than preaxial. The body weight is mainly transmitted through the radius on to the robust ovoid radiale. The extension and twist of the foot during the stride is executed through the ulna articulating with a flattish plate-like ulnare supported postaxially by the pisiforme and preaxially by a laterally uncompressed intermedium.

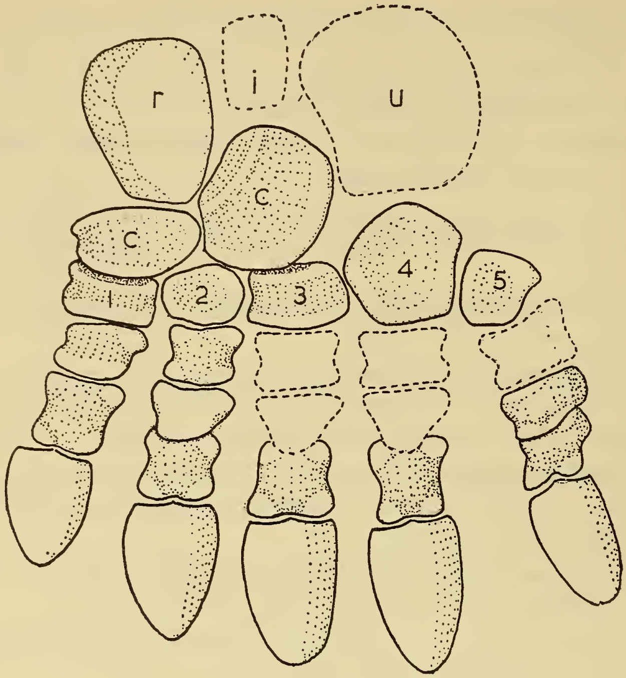

FIG. 1. *Struthiocephalus* sp. SAM 12226 × ⅓
Dorsal view of left manus as restored.

In the middle of the foot there are two centralia, of which the proximal one is the larger, circular in outline; the distal or inner centrale is oval in outline.

There are five distalia of which the fourth is the largest; the first three are broader than long and the other two approximately as long as broad.

The first four metacarpals are very short, but the fifth is quite a large bone.

The digital formula is 2, 3, 3, 3, 3. In each digit the proximal phalanx is very short; in the last four digits the second phalanx is slightly longer.

The terminal or ungual phalanges are broad and carried broad, slightly convex nails.

Titanosuchia (Fig. 2)

In the Titanosuchia even less material of the manus is available. In SAM K249 a number of disarticulated foot-bones are preserved in very good condition but reassembly as in the figure is an act of faith. As reassembled there are three proximal, two central and five distals in the carpus and the digital formula 2, 3, 3, 3, 3.

The radiale is a strong bone oval in outline and both the intermedium and proximal central are laterally compressed elements. A pair of beautifully preserved ulnaria are preserved. The ulnare is a robust bone with large, well-

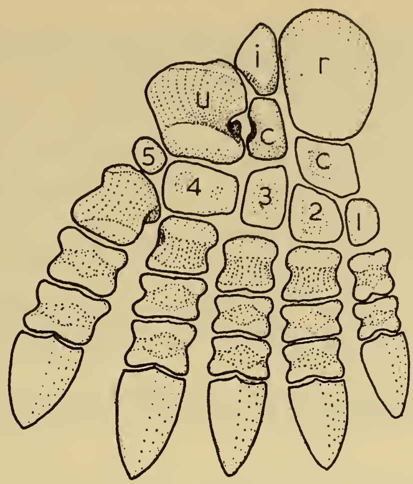

FIG. 2. *Parascapanodon* sp. SAM K249 × $\frac{1}{6}$
Dorsal view of right manus as restored.

developed convex distal as well as proximal articulatory faces; dorsally the surface is shallowly concave and ventrally deeply concave; medially the face is deeply excavated and with a similarly excavated lateral face of the contiguous centrale a long tube is formed to house the penetrating carpal nutritive and innervating vessels.

The fourth distal is the largest of the distalia. The metacarpals are very short and have well modelled convex faces both proximally and distally. The fifth metacarpal is large and broad.

Anteosauria (Fig. 3)

From the *Tapinocephalus* zone I have only one specimen of the Anteosaurs—the type of *Micranteosaurus parvus*—in which the forefoot is preserved. With better technical equipment now available I have prepared the specimen further and with increased knowledge of the structure in related forms I wish to correct the misinterpretation I made in my account of 1954.

In the proximal row of the carpus there were three bones. The ulnare is a flattened element with oval proximal and distal articulatory facets; the outer edge is thin but the inner thickened and rounded, lying preaxially of the ulnare is the intermedium; as preserved it is a thin bone showing a large, flat upper face, but it is possible that it has fallen out of position and would then actually be a laterally compressed bone. Preaxially lies what appears to be a pear-shaped element. I interpret this as a proximal rounded radiale with the distal part actually a central. The lateral central is not preserved.

There are five distals of which the fourth is a large bone with a roughly rectangular upper face. The other distals are pebble-like.

All five metacarpals are preserved; they are all elongated bones with expanded ends and a constricted shaft. They increase in size from 1 to 5, with the fifth a robust bone and the first quite feeble.

The phalanges of only four digits are preserved. The phalangeal formula is 2, 3?, 4, 3, 3, with the third digit the longest and the fourth and fifth only slightly shorter. The first digit is short and feeble. The purchase of the foot thus lies mostly in the postaxial part of the foot.

The proximal phalanges of the last three digits have greatly expanded proximal ends.

The third phalanx of the third digit, although smaller than the first and second phalanges, is not much reduced and apparently not in the process of being lost.

The terminal phalanges are narrow and pointed and would have carried sharp curved claws.

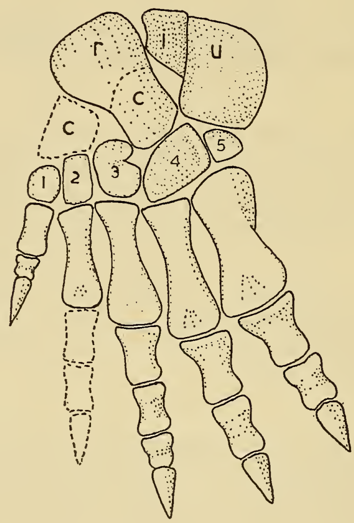

FIG. 3. *Micranteosaurus parvus*. Type. SAM 4323 × ½
Dorsal view of left manus as restored.

In *Titanophoneus*, Orlov found the carpal formula to be 3, 2, 5, with the intermedium laterally compressed and the fourth distal enlarged. The first metacarpal is small and short and from the second to the fifth became progressively longer with the fifth a quite stout bone with expanded ends. Orlov gives the digital formula as 2, 3, 3, 3, 3, with the second phalanx of the fourth digit showing proximally what looks like an epiphysis, which may represent an additional phalanx fused to it. No such structure is shown in the third digit.

The reduction in the number of phalanges in the third and fourth digits has thus followed a different course in *Titanophoneus* and *Micranteosaurus*, with the condition in the latter more primitive than in the former.

The purchase of the foot lies more postaxially in *Titanophoneus* than in *Micranteosaurus*.

Hindfoot

Tapinocephalia (Figs. 4–6)

I have 5 calcanei, 3 astraguli, a number of disarticulated metatarsals and phalanges and one nearly complete pes available for study. In Romer's Chicago specimen of *Moschoides* there is a complete left pes.

In SAM 12226 (fig. 4) it is seen that the proximal bones of the tarsus are very well developed, but the central and distal tarsals fairly weak. The metacarpals and digits are short with the fourth digit slightly the longest and the purchase of the foot mostly postaxial. The digits of the hindfoot are weaker than those of the forefoot.

The proximal row of the tarsus is formed by a robust astragalus and a large flattened disc-like calcaneum.

The astragalus is a strong element of peculiar shape; it is thick, a little longer than broad. In its anterior part the dorsal surface is convex postaxially

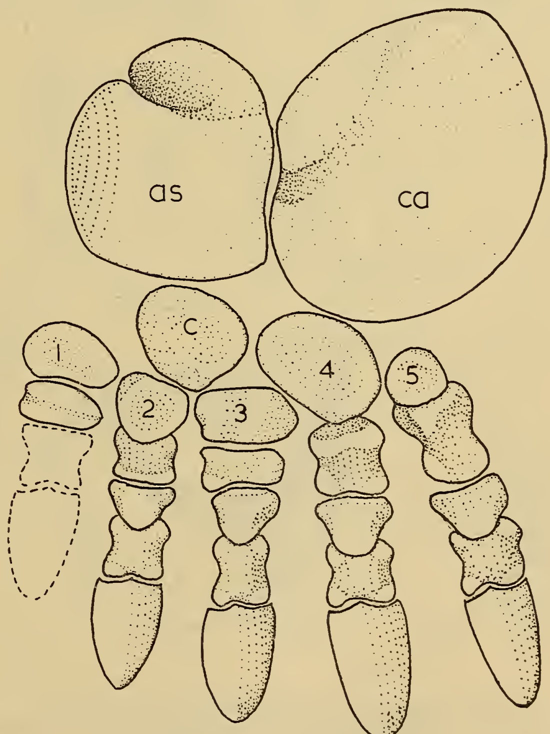

Fig. 4. *Struthiocephalus* sp. SAM 12226 × $\frac{1}{3}$
Dorsal view of left pes as restored.

and hollowed out towards its preaxial edge. The convex surface covered with a thick cartilage is for the reception of the tibia. Proximal of the tibial facet lies an obliquely directed deep groove, which forms a deep proximal incisure extending round the bone and continuing across the ventral surface as a deep groove connecting with the groove on the postaxial surface of the bone. Proximal to this groove the astragalus carries a strong facet for the fibula facing proximo-postaxially.

The concave postaxial face of the astragalus faces an incisure on the calcaneum thus forming a passage for the vessels passing through the tarsus. Distally the surface of the astragalus is convex and this facet for the central tarsal carried a thick cartilage.

The calcaneum is a large flattened bone oval in outline. Its outer and distal edges are rounded and fairly thin. Proximo-preaxially this disc-like element is thickened and here carries an oval facet which receives a part of the distal facet of the fibula. Distally of this thickening there is a shallow groove, which, extending to the preaxial face, lies opposite to the concavity on the astragalar opposing face.

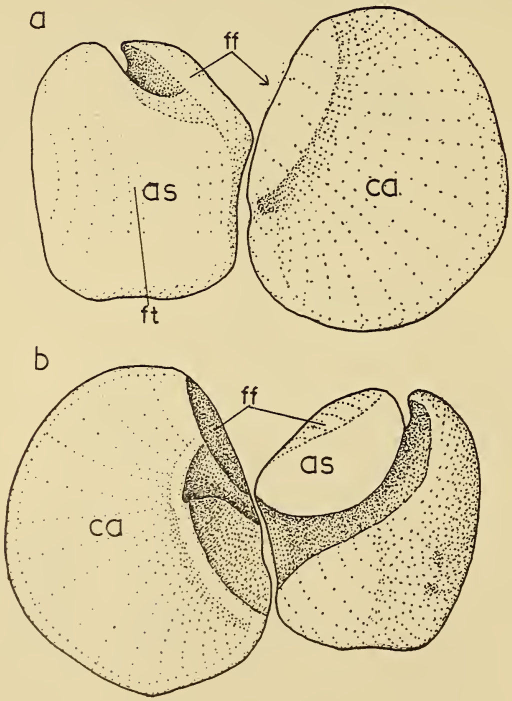

Fig. 5. Tapinocephalid proximal row of tarsals × $\frac{1}{3}$

a—dorsal view b—ventral view

As—astragalus of SAM K201 ff—facet for the fibula

Ca—calcaneum of SAM 12065 ft—facet for the tibia

The single centrale is a fairly large rounded bone lying between the astragalus and the second and third distalia.

There are five distal tarsals of which the fourth is the largest.

The first three metatarsals are very short, but the fourth and especially the fifth are larger and look more like normal metacarpals.

The first phalanges are small bones roughly triangular in shape with the apices distally articulated with the second phalanges. The second phalanges are somewhat larger and have expanded ends and a waist.

The terminal phalanges are broad, slightly curving bones carrying a flat nail.

The digital formula is 2, 3, 3, 3, 3, with the toes of nearly equal length, but the first is the shortest with the fourth only slightly longer than the other three.

In figure 5 the system of grooves in both astragalus and calcaneum are well shown in ventral view. These grooves probably housed tendons associated with the tarsal joint which apparently functioned in a most peculiar manner and difficult to understand. I have attempted in figure 6 to show the peculiar action of the ankle joint.

In a. the leg is shown at the completion of the swing forwards with the toes just about to make contact with the ground. In this position it is evident that the fibula has its bipartite distal facet in contact with the facet on the astragalus

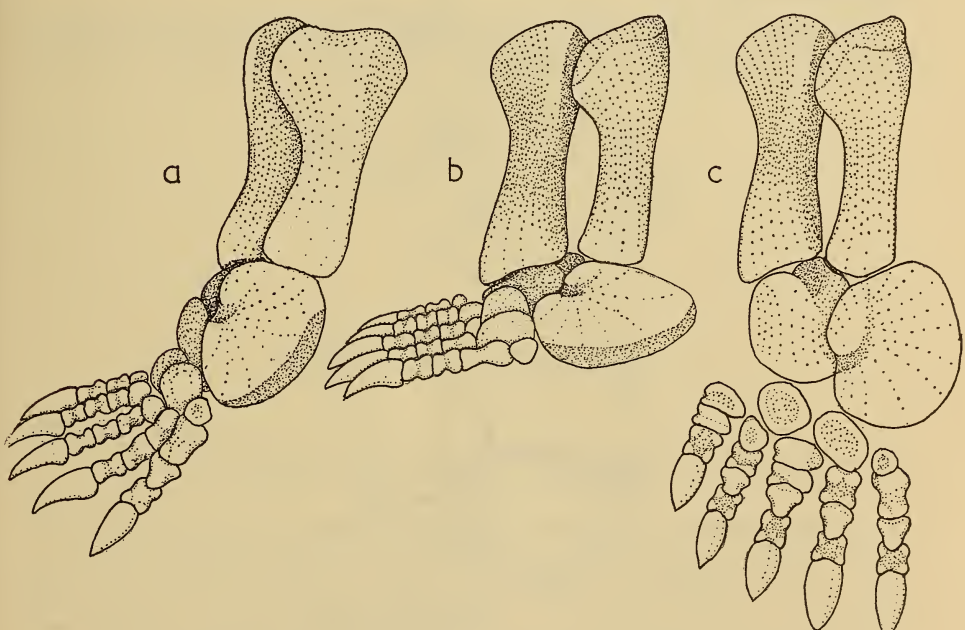

Fig. 6. Tapinocephalid lower hind-limb showing ankle joint in three positions.

a—at completion of the forward swing
b—standing and carrying body weight
c—at completion of the stride

and the facet on the calcaneum, whereas the distal tibial facet is not making contact with the facet on the dorsal face of the astragalus and is in fact out of articulation but held by tendons.

In b. the foot is in the standing position with the body weight transmitted along the long axis of the tibia on to the dorsal facet of the astragalus. In this position it is evident that the distal facets of the fibula are not making contact with the facet on the astragalus nor with the facet on the calcaneum and are in fact out of articulation, but held by tendons only.

In c. the foot is lifted off the ground at the completion of the backward swing of the foot. The body weight is taken off the foot and the astragalus moved away from its contact with the distal facet of the tibia. But the fibula is in contact with the facet on the astragalus and the facet on the calcaneum. Everything is now ready for the forward stride with the foot in position to be swung forwards and twisted by rotation of the fibula on its long axis to assume its contact with the ground position.

If the above representation of the action of the ankle joint is anywhere near being correct, the presence of strong tendons is necessary and these could be housed in the grooves present on both astragalus and calcaneum. I am not so rash as to attempt any description of the mechanism involved.

Titanosuchia (Figs. 7–9)

In addition to the proximal tarsal elements of *Jonkeria* described by Broom and the calcaneum erroneously labelled *Tapinocephalus* by Gregory, I have half

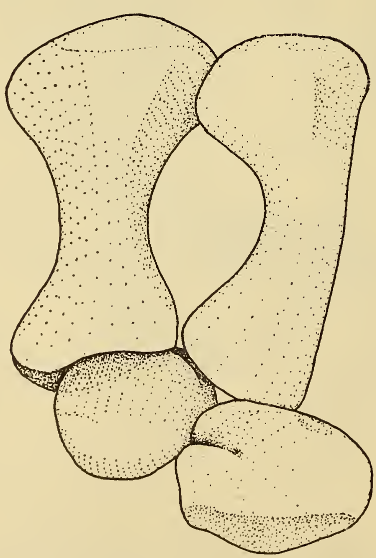

Fig. 7. *Parascapanodon* sp. K249 × $\frac{1}{8}$
Dorsal view with tibia in and fibula out of articulation.

a dozen good astragali and a couple of good calcanei of *Parascapanodon*.

Both the astragalus and calcaneum in Titanosuchians are very similar in essential structure to the corresponding elements as described above in the case of the Tapinocephalians. They can be distinguished from the latter in that the astragalus is a large and heavier bone and the calcaneum is larger, and in the details of the ventral and penetrating grooves.

In figure 7 the tibia is shown in articulation, in figure 8 the fibula is articulated to both astragalus and calcaneum and in figure 9 the bones are shown in ventral view with the fibula articulated.

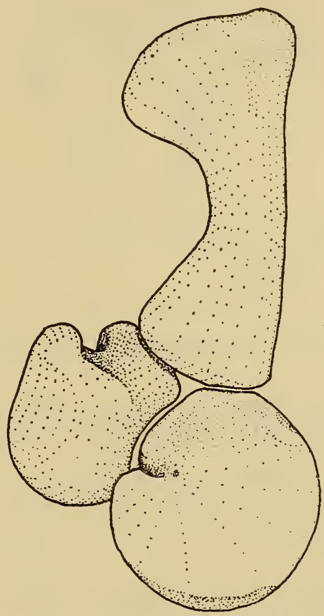

FIG. 8. *Parascapanodon* sp. K249 × $\frac{1}{6}$
Dorsal view with fibula in articulation.

Anteosauria (Fig. 10)

In the type specimen of *Micranteosaurus parvus* there is an incomplete foot preserved.

The calcaneum is a typical Therapsid flattened disc-like bone—thin in its middle part and with a thin postaxial edge. Both the dorsal and ventral surfaces are concave centrally with a thickened proximal and distal end where good convex facets are developed for the fibula and centrale and second distal. Its preaxial edge facing the astragalus is excavated to form a passage for the penetrating vessels. The system of grooves so typical of the Tapinocephalia and Titanosuchia are not developed.

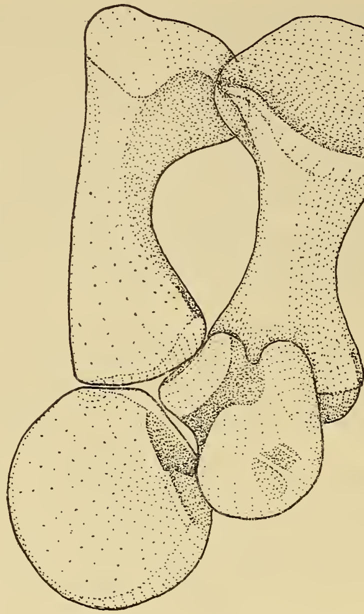

Fig. 9. *Parasapanodon* sp. K249 × $\frac{1}{6}$
Ventral view with fibula in articulation.

The astragalus is a stout bone and is quite different to the specialized bone seen in the Tapinocephalia and Titanosuchia. The major part of its dorsal surface is formed by a well-developed rounded articular facet for the tibia. Anterior to this facet lies a groove which flows into the incisure on the postaxial face lying opposite to that on the calcaneum. Anterior to this groove an oval knoblike thickening apparently articulates with the central and the second distal. The ventral surface of the astragalus appears to be convex without grooves.

There probably were five distals and also probably a central, but none are preserved, in their position lie two displaced phalangeal elements.

The five metatarsals are elongated bones with a waist and expanded ends. The first is quite small and the others progressively increase in size, with the fifth a strong element.

The first digit is complete and the first phalanx short with expanded ends and a waist; the terminal phalanx is sharp and narrow and carried a claw. Only the proximal ends of the first phalanx of the second and third digits are preserved. I presume that the digital formula was 2, 3?; 4?; 3?; 3?, as in the forefoot.

The foot was apparently weak preaxially and strong postaxially.

The pes of *Micranteosaurus* is very similar to that of the Russian *Titanophoneus*, but there Orlov found no centrale and a digital formula 2, 3, 3, 3, 3.

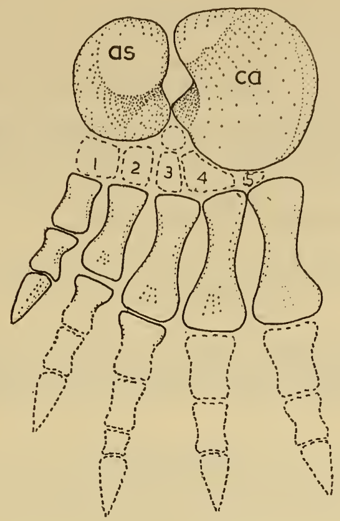

FIG. 10. *Micranteosaurus parvus*. Type. SAM 4323 × ½
Dorsal view of left pes as restored.

DISCUSSION

The Dinocephalian feet are more primitive than those of the Sphenacodonts in that the first carpal is not elongated, but otherwise they are definitely more advanced.

The digital formula in Sphenacodonts is 2, 3, 4, 5, 3—with a well-developed first digit, a great increase in length from second to fourth digit and a comparatively short fifth digit.

In the Dinocephalia the phalanges of the three middle toes are reduced in number, the first digit is weaker, the three middle digits are shortened and tend to become equal in length and the fifth digit becomes relatively stronger. *Micranteosaurus*, with a digital formula 2, 3, 4, 3, 3, has the most primitive feet; then comes *Titanophoneus* in which the fourth digit in the forefoot shows a fusion of two phalanges to produce the formula 2, 3, 3, 3, 3, which also obtains in the Titanosuchia and Tapinocephalia.

Proximally the tarsus is still fairly primitive in the Anteosaurs and becomes more specialized in the Titanosuchians and Tapinocephalians.

The distal phalanges in Anteosaurs still carried a claw as one would expect in carnivores, whereas in the Titanosuchians and Tapinocephalians, which were herbivores, the nails are flattened.

The direction of development in the Dinocephalia seems to have been away from a crawling habit with sprawling feet to a more walking habit with the feet drawn in closer to the median line of the body.

Summary

Descriptions and figures are given of the manus and pes of the Dinocephalia of the *Tapinocephalus* zone in South Africa. Owing to the nature of the preservation of the dinocephalian material in this zone only eighteen of more than two hundred specimens included bones of the feet, and this account is based on these specimens. There are indications that the Dinocephalia show a development from a crawling to a walking habit.

Acknowledgement

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